Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States

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Atmospheric nitrogen (N) deposition has been shown to decrease plant species richness along regional deposition gradients in Europe and in experimental manipulations. However, the general response of species richness to N deposition across different vegetation types, soil conditions, and climates remains largely unknown even though responses may be contingent on these environmental factors. We assessed the effect of N deposition on herbaceous richness for 15,136 forest, woodland, shrubland, and grassland sites across the continental United States, to address how edaphic and climatic conditions altered vulnerability to this stressor. In our dataset, with N deposition ranging from 1 to 19 kg N·ha^{-1}·y^{-1}, we found a unimodal relationship; richness increased at low deposition levels and decreased above 8.7 and 13.4 kg N·ha^{-1}·y^{-1} in open and closed-canopy vegetation, respectively. N deposition exceeded critical loads for loss of plant species richness in 24% of 15,136 sites examined nationwide. There were negative relationships between species richness and N deposition in 36% of 44 community gradients. Vulnerability to N deposition was consistently higher in more acidic soils whereas the moderating roles of temperature and precipitation varied across scales. We demonstrate here that negative relationships between N deposition and species richness are common, albeit not universal, and that fine-scale processes can moderate vegetation responses to N deposition. Our results highlight the importance of contingent factors when estimating ecosystem vulnerability to N deposition and suggest that N deposition is affecting species richness in forested and nonforested systems across much of the continental United States.

nitrogen deposition | plant species richness | diversity | soil pH | climate

Global emissions of reactive nitrogen (N) to the atmosphere and subsequent deposition into terrestrial ecosystems have tripled in the last century (1). This N deposition has been identified as a threat to plant diversity (2–4), and plant diversity is linked to ecosystem stability (5), productivity (6), and other ecosystem services (7). Elevated nitrogen inputs have been shown to cause decreases in species richness over time in small plot experiments (8–10) and in regional gradient studies in Europe (11, 12). Although these studies and others have led to some generalizations about the impacts of N deposition on plant diversity, most of these studies have focused on grassland ecosystems and/or, in the United States, have been fine-scale field experiments where N is added experimentally as fertilizer. Thus, translation of these findings to nongrassland systems or to large regions of the United States may not be appropriate. Unlike grasslands, where elevated N has often led to light limitations and subsequent competitive exclusion (13), plant growth in the herbaceous layers of forest understories is typically primarily light-limited (14) regardless of the extent of N inputs. Moreover, soil chemistry can be heterogeneous, influencing the potential of soil acidification by nitrogen deposition (15). In most arid ecosystems, moisture may be more important than nutrients in controlling plant growth during the growing season (16, 17). Finally, the level of N input at which diversity is first impacted (18) is often unknown for many regions because most studies use a fairly coarse experimental approach to estimate thresholds of response or have been conducted where there have already been high inputs of N for decades (e.g., Northern Europe). To address these critical gaps in our knowledge of continental-scale relationships between N deposition and plant diversity, we used data from herbaceous ground-layer communities within 15,136 forest, woodland, shrubland, and grassland sites spanning N deposition gradients across the continental

Significance

Human activities have elevated nitrogen (N) deposition and there is evidence that deposition impacts species diversity, but spatially extensive and context-specific estimates of N loads at which species losses begin remain elusive. Across a wide range of climates, soil conditions, and vegetation types in the United States, we found that 24% of >15,000 sites were susceptible to N deposition-induced species loss. Grasslands, shrublands, and woodlands were susceptible to species losses at lower loads of N deposition than forests, and susceptibility to species losses increased in acidic soils. These findings are pertinent to the protection of biodiversity and human welfare and should be considered when establishing air quality standards.

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United States. More specifically, we assessed how covarying climate and edaphic factors affected ecosystem vulnerability to N deposition.

Nitrogen inputs can increase diversity, decrease diversity, or leave diversity unchanged, contingent on a host of associated ecosystem factors. Biodiversity can be reduced through several general mechanisms (4), including but not limited to (*i*) release from N limitation that leads to increased aboveground production, reduced light availability, and ultimately competitive exclusion (13, 19) and (*ii*) soil acidification and associated cation depletion and imbalances that lead to recruitment inhibitions (20, 21). The importance of N limitation likely declines in arid areas that are more moisture-limited or in warm, wet areas favoring high net N mineralization, either one of which may reduce the importance of external N inputs. In such cases, N may be less limiting to plant growth, and therefore communities are less responsive to additional N deposition (2). Conversely, enrichment may increase biodiversity in extremely N-poor environments where release from N limitation does not result in competitive exclusion (22, 23) or where soils have a high pH resistant to soil acidification (11, 24).

Because N enrichment can affect plant diversity through multiple pathways and environmental contingencies, we investigated whether N deposition is a widespread threat to plant species diversity or whether some vegetation types or environments are more vulnerable than others. We compiled herbaceous plant species composition data from existing datasets (Table S1) that included 15,136 sites and 3,852 herbaceous species from across the continental United States. At each site, we calculated species richness, the total number of unique species per plot, a commonly used metric of diversity (25). We then extracted geospatial estimates (Table S2) of N deposition, annual precipitation, mean annual temperature, and soil pH for each site. As in several previous studies in Europe (11, 12, 26), we used a correlative approach that cannot show direct causality but can nevertheless provide insight into the mechanisms involved in, and communities most susceptible to, loss of diversity as a result of N deposition. First, we analyzed relationships between plant species richness and N deposition involving interactions with precipitation, temperature, and soil pH within two broadly defined vegetation types (closed canopy forest vs. open canopy grasslands, shrublands, and woodlands). We then examined the same set of predictors within gradients defined by unique combinations of specific vegetation communities and source datasets that spanned an adequate range of N deposition (*Methods* and Table S3).

Table 1. Parameter coefficients for species richness from median quantile regressions

Name	Open canopy (±1 SE)	Closed canopy (±1 SE)
Intercept	14.9 (3.42)*	13.6 (2.55)*
N	4.69 (0.60)*	0.449 (0.33)^{n}
N^2	−0.494 (0.02)*	−0.125 (0.01)*
pH	−2.17 (0.46)*	−1.49 (0.37)*
Precip	−0.011 (0.002)*	−0.003 (0.001)*
Temp	−0.059 (0.18)^{n}	−0.321 (0.04)*
N:pH	0.475 (0.07)*	0.543 (0.04)*
N:precip	0.002 (0.001)*	NA
N:temp	−0.073 (0.03)$^{+}$	NA

Regressions represent herbaceous plant species richness response to N deposition (kg·ha^{-1}·y^{-1}; quadratic), soil pH, total annual precipitation (mm), average annual temperature (°C), and interactions of N (deposition) with pH, precipitation, and temperature. An NA (not applicable) indicates that term didn't appear in best model. Sample size is 11,819 sites for closed canopy (deciduous forest, evergreen forest, and mixed forest) and 3,317 sites for open canopy (grassland, shrubland, and woodland). Level of significance is indicated as follows: $^{n}P \geq 0.05$, $^{+}P < 0.05$, or $*P < 0.001$.

Results and Discussion

National-Scale N Deposition Critical Loads and Exceedances Analyses. At a national scale, separating sites into open canopy (grassland, shrubland, and woodland) versus closed canopy (forested) vegetation types, we found that herbaceous plant species richness was best explained by N deposition (R^1 coefficient of determination = 0.10 and 0.05 for open and closed vegetation, respectively), followed by soil pH (R^1 = 0.02 and 0.04 for open and closed vegetation, respectively), temperature (R^1 = 0.04 and 0.01 for open and closed vegetation, respectively), and precipitation (R^1 = 0.02 and 0.004 for open and closed vegetation, respectively). Regression analyses incorporating N deposition interaction effects with other predictors (Table 1) showed strong hump-shaped relationships between herbaceous plant species richness and N deposition in open canopy vegetation (Fig. 1*A* and Fig. S1 *A* and *B*). In open-canopy

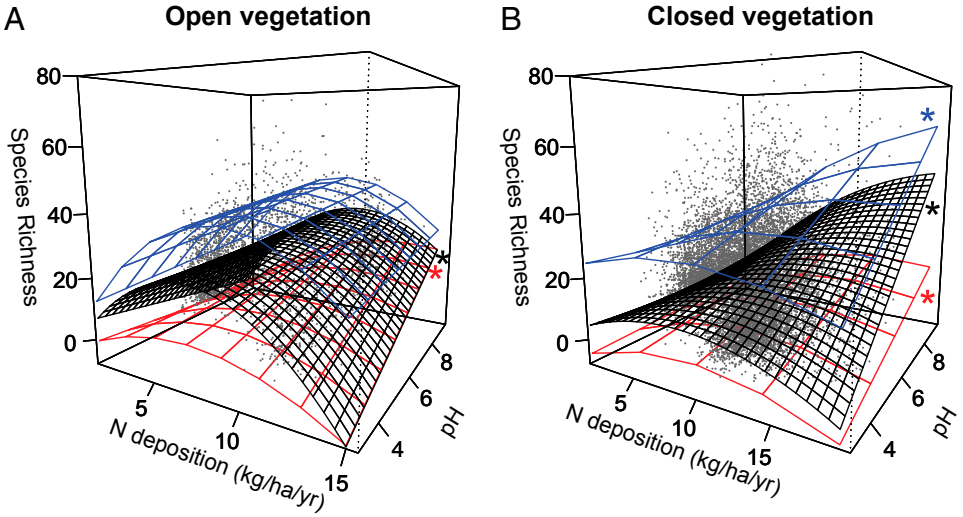

Fig. 1. Herbaceous plant species richness relationships with N deposition. Raw data points (n = 15,136 sites) are gray. Surface plots represent 0.1 (red), 0.5 (median; black), and 0.9 (blue) quantile regression models (median parameters in Table 1) fitted to 3,317 open sites (combined grassland, shrubland, and woodland) (*A*) and 11,819 closed canopy sites (combined deciduous, evergreen, and mixed forests) (*B*), as influenced by soil pH. Asterisks indicate significant interactions ($P < 0.05$).

Table 2. Critical loads (CLs) of N deposition for herbaceous plant species richness

Vegetation	CL expression (partial derivative of species richness equation)	CL (kg N·ha^{-1}·y^{-1}) Mean[†]	Range[†]	Range of 95% CI[‡]	CL error[§]
Open canopy vegetation	[4.690 + (0.475 · (soil pH)) + (0.0018 · (mm of precip.)) + (−0.073 · (temp. (°C)))]/(−2 · −0.494)	8.7	7.4–10.3	6.4–11.3	−4.5%, 4.8%
Closed canopy vegetation	[0.449 + (0.543 · (soil pH))]/(−2 · −0.125)	13.4	7.9–19.6	6.8–22.2	−6.2%, 7.7%

The critical load (CL) expression is derived using the partial derivative with respect to nitrogen of the species richness equation in Table 1, and then evaluated locally with site-specific soil pH, precipitation, and temperature values.
[†]Mean and range of CLs across sites, reflecting variation in soil pH, precipitation, and temperature variables across sites but not uncertainty in coefficient estimates.
[‡]Range of CL 95% confidence interval endpoints across sites (Fig. S3), reflecting both ecological variability (soil pH and climate variables) and uncertainty in coefficient estimates, with the latter calculated from the 2.5th and 97.5th percentiles of 10,000 Monte Carlo simulations of coefficient uncertainty.
[§]Average of the site-specific CL % errors, calculated from the lower and upper endpoints of the 95% confidence interval of Monte Carlo simulations of coefficient uncertainty repeated at each site.

vegetation, richness declined at lower N deposition levels in more acidic soils—declining with N deposition above 6.5 kg·ha^{-1}·y^{-1} at a soil pH of 4.5, and declining with N deposition above 8.8 kg·ha^{-1}·y^{-1} at a soil pH of 7 (Fig. 1*A*). In closed-canopy conditions, the interaction of N deposition with soil pH was even stronger: At a soil pH of 4.5, richness began declining when N deposition exceeded 11.6 kg·ha^{-1}·y^{-1}, whereas at the highest pH (8.2) there was no evidence of a decline (Fig. 1*B*). In closed-canopy communities, there was no significant interaction of temperature (Fig. S1*C*) or precipitation (Fig. S1*D*) with N deposition in most quantiles.

Our results demonstrate for the first time, to our knowledge, across a wide spatial domain that multiple mechanisms may

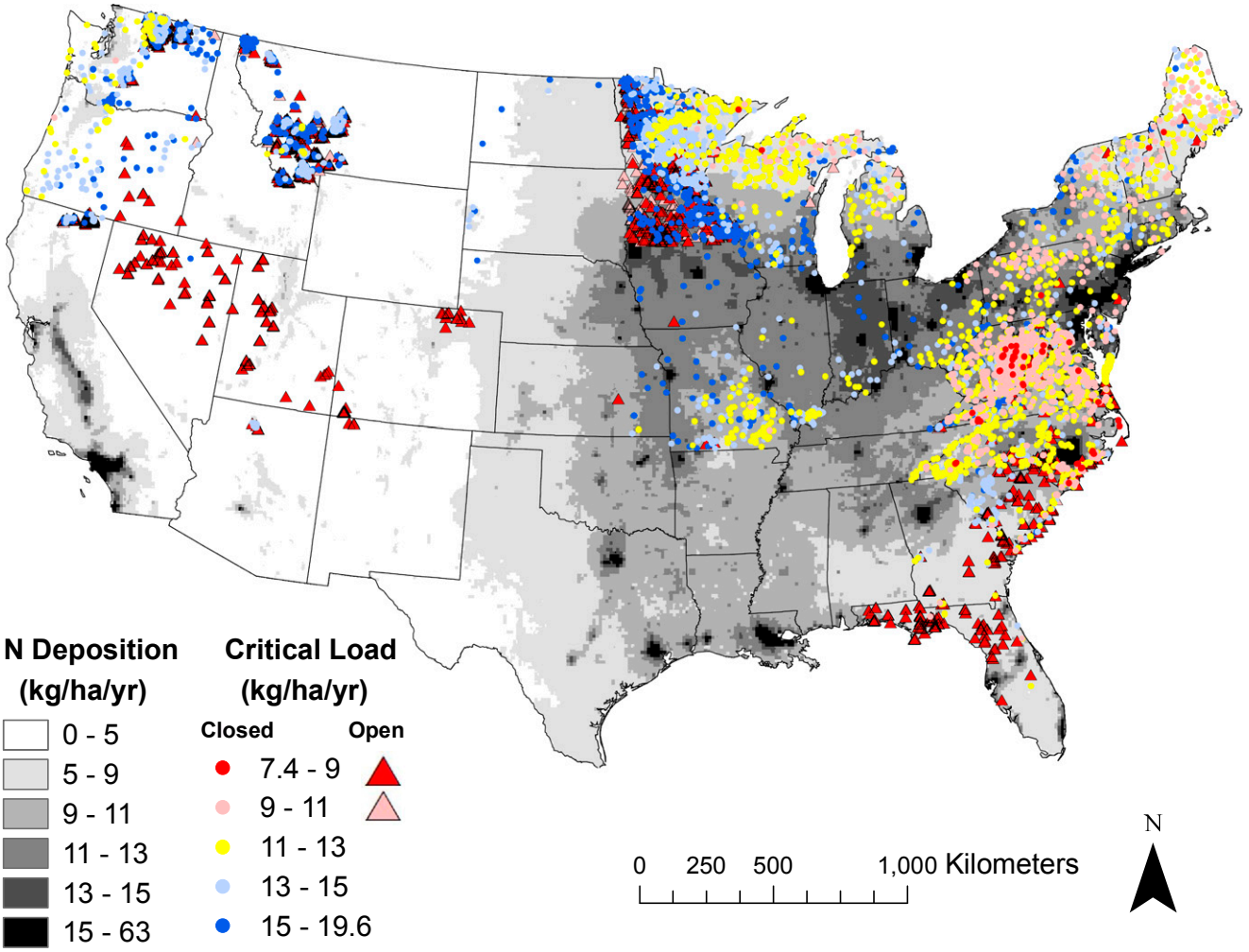

Fig. 2. Nitrogen deposition (gray-scale) and critical loads for nitrogen deposition based on total graminoid plus forb species richness (colored symbols). The 3,317 open sites (combined grassland, shrubland, and woodland vegetation types) are portrayed with triangles, and the 11,819 closed canopy sites (deciduous, evergreen, and mixed forests) are portrayed with circles. Background deposition values are the average of 27 y of wet deposition (NADP 1985–2011) plus the average of 10 y of dry deposition (CMAQ 2002–2011). Other variation in critical loads is due to the other predictor variables (soil pH, temperature, and precipitation).

operate to influence the response of plant species richness to N deposition. A decline in species richness with N deposition at low soil pH in both open and closed canopy systems is consistent with the soil acidification mechanism of species loss (20). At higher soil pH, the patterns found in the two systems diverged. Increased species richness with N deposition in the shaded forest understory is consistent with release from the soil acidification mechanism combined with a limited potential for competitive exclusion through shading—because most understory forest species are already well adapted to shady conditions. In open canopy systems, some species are not well adapted to shady conditions, meaning that, even though release from soil acidification had occurred at higher pH, competitive exclusion from light limitation may still have been a potential factor affecting plant richness (13).

Critical loads of N deposition based on changes in herbaceous plant species richness are defined as the point at which species losses begin to occur (18) and are calculated here by taking the partial derivative with respect to nitrogen of the surfaces in Fig. 1 (and Table 1) and solving for N (*Methods*). Critical loads were generally much lower in open grasslands, shrublands, and woodlands than in closed-canopy forests (Table 2, Fig. 2, and Fig. S2). Critical load estimates were contingent on soil pH (and in open vegetation on climate as well), but parameter uncertainty in the critical load estimates was relatively modest (Table 2 and Figs. S3 and S4). When we subtracted N deposition critical load estimates from N deposition values, we found that 5% of sites had exceedances of 3–8 kg·ha^{-1}·y^{-1} and 19% had exceedances of up to 3 kg·ha^{-1}·y^{-1} (Fig. S5). For alternate exceedance calculations, a benefit-of-doubt approach [using upper limit of 95% confidence interval (CI) of the critical load] yields a maximum exceedance of 8.3 kg·ha^{-1}·y^{-1} and 18% of sites having positive exceedances whereas a precautionary approach (using lower limit of 95% CI of the critical load) yields a maximum of 9.6 kg·ha^{-1}·y^{-1} and 29% of sites with positive exceedances. If methods change N deposition estimates, then critical loads would also increase or decrease by that same percentage.

When we applied national-scale critical loads equations (Table 2) to specific level 1 ecoregions, we were able to refine (Table S4) previous estimated critical loads (18) as a consequence of using many more data than were previously available across a wider range of environmental conditions. We emphasize that all critical loads of N deposition presented here are for total herbaceous plant species richness from the national analysis and that critical loads may be lower for specific species (23), functional groups (4), or ecoregions.

Furthermore, when we calculated critical load estimates (Table 2) for specific sites using our national-scale equations (Table 1), we found that they were consistent with experimental data from long-term N additions. Our critical load estimate of 8.4 kg N·ha^{-1}·y^{-1} for grassland at the Cedar Creek LTER site was consistent with the critical loads estimated there using statistical extrapolation of results from a fertilization experiment (95% inverse prediction interval of 7.3–15.8 kg N·ha^{-1}·y^{-1}) (10). Likewise, our estimated critical load of 11.8 kg N·ha^{-1}·y^{-1} for forest in the Fernow Experimental Forest was consistent with the interpretation (27) that ambient N deposition already exceeded critical loads before the initiation of experimental additions at Fernow. This consistency of experimental and gradient results strengthens our confidence in our critical load estimates for sites without long-term experimental data.

Finer Scale N Deposition Gradients Within Specific Vegetation Communities. Having just demonstrated relationships between plant species richness and N deposition at a national scale, we now shift our focus to the community scale at which many local land management activities are directed. Within community-scale deposition gradients, we again found that relationships between plant species richness and N deposition were often conditional on soil and climate covariates. Plant species richness declined as N deposition increased in 36.5% of the 44 studied gradients (16% unconditional, 20.5% conditional on a covariate), increased with N deposition in 18% of the gradients (4.5% unconditional, 13.5% conditional), and showed no relationship with N deposition in 45.5% of gradients (Fig. 3). Most of the gradients where species richness increased with N deposition had N deposition averaging 3 kg N·ha^{-1}·y^{-1} or less (Fig. 4). Overall, plant species richness was more likely to decline with increasing N deposition along gradients with more acidic soil conditions (Fig. 4*A*), or warmer (Fig. 4*B*), wetter (Fig. 4*C*) climates, broadly consistent with the national analysis. Both the community-level and national-level analyses showed decreases in more acidic conditions, and although the community-level analysis showed declines under warmer conditions, that relationship was present only for open canopy systems for the national analysis. This restricted gradient analysis was possible only in the subset of vegetation types that spanned an adequate N deposition range (Table S3), but its power lies in the capacity to detect relationships missed by national-scale analyses, and the restriction to datasets within similar methodologies and vegetation types to control for any potential spurious relationships.

We demonstrate the context dependency of N deposition effects using the three forested vegetation types (*Acer-Betula* alliances, *Quercus alba* alliances, *Pseudotsuga menziesii* alliances) that were represented in more than three separate gradients (Table S5). In these cases, species richness declines were more readily detected where precipitation and temperature were highest, or where N deposition reached or exceeded 7.5–9.5 kg·ha^{-1}·y^{-1}. Among the four *Acer - Betula* forest gradients, only the gradient with the highest precipitation and temperature showed an unconditional species richness decline with N deposition. Among the six *Q. alba* forest gradients, only the two gradients where N deposition was always greater than 9.5 kg·ha^{-1}·y^{-1} showed a species richness decline with N deposition. Finally, among the four *P. menziesii* forest and woodland gradients, we observed increases in richness in the three gradients where deposition was always below 4.6 kg·ha^{-1}·y^{-1}, but, in the gradient with up to 7.5 kg·ha^{-1}·y^{-1}, a species decline emerged. Shifts in relationships for the same vegetation type along different N deposition ranges were consistent with the curved response surfaces illustrated in Fig. 1.

In grasslands and shrublands, we hypothesized that the competitive exclusion mechanism of N deposition-induced species loss would be strong because there is greater potential for some herbaceous species to shade or grow faster than other non–shade-tolerant or slower growing herbaceous species. Consistent with this hypothesis, one of three shrubland gradients showed an unconditional decrease in plant species richness with increasing N deposition, even though all shrubland gradients experienced N deposition of 5 kg·ha^{-1}·y^{-1} or less (Table S5). Shrublands experiencing higher N deposition have shown even stronger responses (e.g., native species richness declines in coastal sage scrub with N deposition beyond 8.7 kg·ha^{-1}·y^{-1}) (28). Grassland species richness declined once N deposition exceeded 8 kg·ha^{-1}·y^{-1} (*Schizachyrium scoparium-Bouteloua curtipendula* and *Andropogon gerardii-Sorghastrum nutans* grasslands in Table S5), consistent with experimental work (10) and a continental-scale study of European grasslands (11).

Scale and Context Dependency of Species Richness Relationships with N Deposition. Our results demonstrate that negative relationships between N deposition and species richness are common, albeit not universal, and that fine-scale processes seem to moderate vegetation responses to N deposition in many areas. This scale-dependency is consistent with the known mechanisms of biodiversity loss (4, 9, 29), all of which may operate simultaneously in ecosystems. At both the national and fine scales, we identified environmental conditions where there was little to no relationship between N deposition and species richness, and conditions under which N deposition increases species richness, which helps place previous work (30, 31) in context, and unifies these conflicting empirical results to ecological theory. We were able

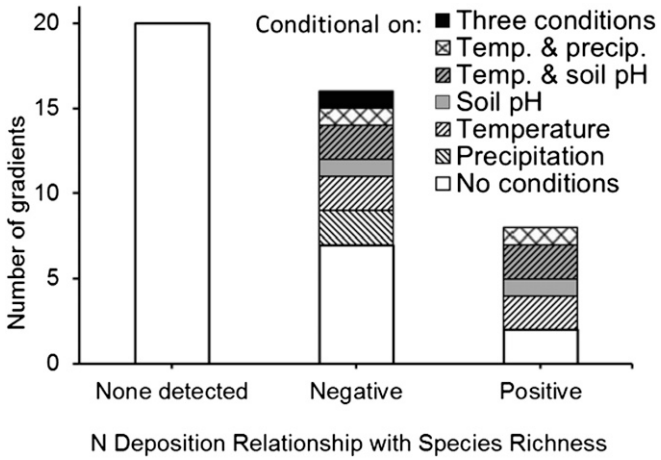

Fig. 3. Summary of relationships between plant species richness and N deposition in 46 gradients. Gradients (uniquely defined by vegetation type and data source) contain 6,807 sites, conditional on soil pH, average annual temperature, annual precipitation, and N deposition interactions with each of the other three predictors. In conditionally negative or positive gradients, the relationship was either negative or positive, respectively, for more than half of the range of the moderating variable(s).

to identify N deposition relationships with species richness by accounting for heterogeneous soil pH and climate factors within distinct vegetation types. As national-scale, high-resolution datasets for other covariates such as herbivory (32) and disturbance history become available, it should be possible to resolve in even finer detail this relationship between N deposition and plant species richness.

Conclusion

Our continental-scale analysis found that the threat of N deposition to herbaceous plant species richness is ecosystem-specific, with some ecosystems more vulnerable than others, and some conditions conferring greater vulnerability. Ecosystems with open vegetation (grasslands, shrublands, and woodlands) had lower critical loads of N deposition (7.4–10.3 kg $N{\cdot}ha^{-1}{\cdot}y^{-1}$) than ecosystems with closed-canopy forest vegetation (7.9–19.6 kg $N{\cdot}ha^{-1}{\cdot}y^{-1}$). Within these broad vegetation groups, declines in species richness along gradients of increasing N deposition were more likely to occur in ecosystems with acidic soils. Climate also interacted with N deposition to help explain species richness, but its influence was less consistent across scales. Increasing the number of N-addition experiments with treatment levels spanning 2–20 $kg{\cdot}ha^{-1}{\cdot}y^{-1}$ and implementing them across the full range of soil pH, climate, and vegetation types that exist on the landscape would be a very welcome complement to the correlative work that we have reported here. In the meantime, our work suggests that the mechanism of competitive exclusion via shading is likely of reduced strength in the comparative shade of forest understories whereas the acidification and competitive exclusion mechanisms are probably more likely to occur synergistically in the high-light environment characteristic of grasslands. We successfully identified ecosystems vulnerable to N deposition and refined herb-based N deposition critical loads (18) by incorporating a broad range of vegetation types, N deposition loads, soil substrates, and climate conditions in our analysis. This identification of vulnerable ecosystems and influential environmental factors is critical for managers to set monitoring and conservation priorities.

Methods

Data Acquisition and Management. We compiled vegetation data from multiple sources (Table S1) because a single standardized national dataset of herbaceous plant species presence and abundance with sufficient spatial coverage and plot density is not available for the United States. We retained only terrestrial sites sampled after 1989 that had a complete inventory of species from graminoid and forb functional groups, quantitative abundance for each plant species, a sampling area of 100–700 m^2, and known geographic coordinates. At each site, we calculated total herbaceous (defined here as forbs and graminoids) plant species richness, a conservative measure because total richness could remain unchanged even as invasive species richness increases and native species richness declines.

We estimated N deposition by adding Community Multiscale Air Quality (CMAQ) model dry deposition estimates to interpolated National Atmospheric Deposition Program (NADP) wet deposition and extracting a value based on coordinates for each site. The CMAQ version 5.0.2 dry deposition estimate was a 10-y average (2002–2011) with 12-km resolution, using models run in 2014 by Robin Dennis at the Environmental Protection Agency (EPA). CMAQ dry deposition estimates, or other comparable estimates with fine resolution, are not yet available at a national scale before 2002. The NADP wet deposition was a 27-y average (1985–2011), which we resampled from the raw 2.33833-km resolution to the 4-km resolution of the Parameter-Elevation Relationships on Independent Slopes Model (PRISM) precipitation data that had been used in the interpolation.

We extracted climate covariates [specifically, average annual precipitation and temperature from 30-y PRISM climate normals (1981–2010)] and obtained soil pH, where available, from the same datasets that supplied vegetation data. If soil data from soil samples colocated with vegetation data were not available, then pH from 1:1 water extracts from the national US Department of Agriculture (USDA) Soil Survey Geographic (SSURGO) database was used. We retained the 15,136 sites with nonmissing species richness and predictor values that met the criteria for analyses at either the national scale (data sources combined but plots filtered based on area) or gradient scale (data sources considered separately).

Data Analysis. For our initial national-scale analysis, we began with all 15,136 sites, and then, based on expected differences in mechanisms, we divided those sites into two broad vegetation types: namely, closed canopy (deciduous forest, evergreen forest, and mixed forest) and open canopy (grassland, shrubland, and woodland) vegetation types. Within each of these two groups, we determined the relative importance of our four primary predictor variables (N deposition, soil pH, precipitation, and temperature) by looking at the R^1 coefficients of determination (based on absolute deviations in quantile regression rather than squared deviations) of b-spline models with and without these four main effects. Next, we examined nonlinear regressions of the 0.50 (median), 0.10, and 0.90 quantiles of total herbaceous plant species richness response to N deposition (quadratic), soil pH, mean annual

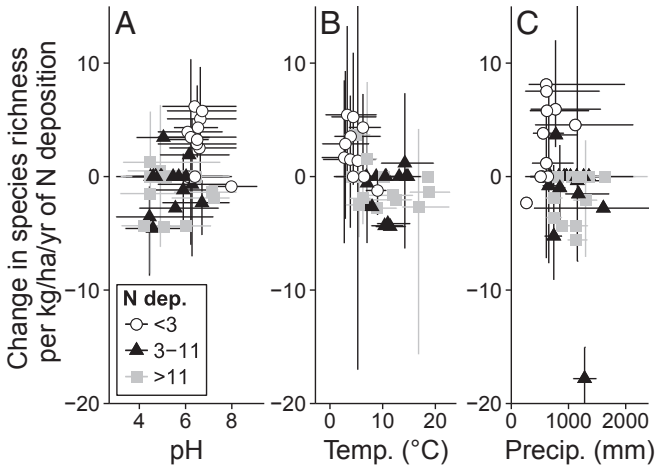

Fig. 4. Magnitude of plant species richness changes associated with N deposition, as moderated individually by (*A*) soil pH, (*B*) average temperature, or (*C*) annual precipitation. Each point, symbolized by the mean N deposition of that gradient ($kg{\cdot}ha^{-1}{\cdot}y^{-1}$), represents an individual gradient with a single narrow vegetation type. Species richness change is calculated as the simple slope of nitrogen deposition from multiple regression coefficients: $\beta_N + (\beta_{N*M} \times M_i)$, where β_N is the parameter for N deposition, β_{N*M} is the parameter for the interaction of N deposition and the moderating variable M, and M_i are the mean (symbol) and range (lines) of the moderating variable M across the gradient. Unlike in Fig. 3, each predictor variable is considered separately.

temperature, annual precipitation, and the two-way interactions involving N deposition (i.e., N × precipitation, N × temperature, and N × soil pH) using the quantreg package of R (version 3.0.2) software. Out of all possible models, we selected the model with the lowest corrected Akaike information criterion (AICc) for each of the two broad vegetation types (Table 1 and Fig. 1).

We used the median quantile regression model with the best AICc to calculate separate critical loads of N deposition for open and closed canopy vegetation. Qualitatively, critical loads of N deposition are defined here as the N deposition threshold at which species richness begins to decline, corresponding graphically to the N deposition level at which a hump-shaped relationship between N deposition and species richness reaches its peak value of species richness. Quantitatively, we calculated critical loads of N deposition by taking the first derivative of the best model with respect to nitrogen and setting that expression to zero, for models with a negative quadratic N deposition term. For critical loads specific to each site, we used the coefficients from the critical load expression and site-specific covariate values. We subtracted critical loads from N deposition to determine exceedances of N deposition critical loads. Three sets of exceedances were calculated, using (*i*) the median point estimates of critical loads, as well as (*ii*) the upper and (*iii*) the lower limits of the 95% CI of the critical loads. Only the exceedances based on the median point estimates of critical loads are presented graphically and in the Abstract.

Further community-scale analyses were focused on individual alliances as defined by the National Vegetation Classification (NVC) (33). We analyzed alliances with deposition gradients with maximum N deposition that was either 2.5 times or 4 $kg{\cdot}ha^{-1}{\cdot}y^{-1}$ greater than minimum N deposition, and that had at least 20 sites from at least one common data source. These gradient criteria reduced the number of sites to 6,807. For each N deposition gradient, we performed multiple regressions of species richness against N deposition, with the same predictor variables and the same model selection procedure as in the national analysis (except that N deposition was only first order).

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